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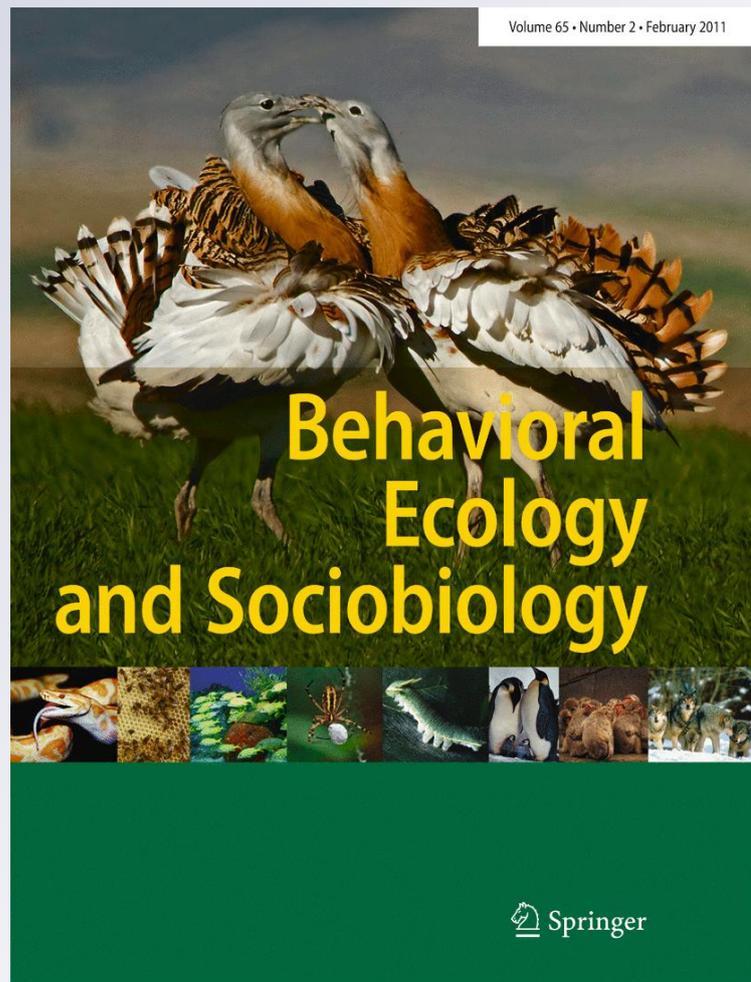
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Within-group spatial position in ring-tailed coatis: balancing predation, feeding competition, and social competition

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Abstract A variety of factors can influence an individual's choice of within-group spatial position. For terrestrial social animals, predation, feeding success, and social competition are thought to be three of the most important variables. The relative importance of these three factors was investigated in groups of ring-tailed coatis (*Nasua nasua*) in Iguazú, Argentina. Different age/sex classes responded differently to these three variables. Coatis were found in close proximity to their own age/sex class more often than random, and three out of four age/sex classes were found to exhibit within-group spatial position preferences which differed from random. Juveniles were located more often at the front edge and were rarely found at the back of the group. Juveniles appeared to choose spatial locations based on feeding success and not predation avoidance. Since juveniles are the most susceptible to predation and presumably have less prior knowledge of food source location, these results have important implications in relation to predator-sensitive foraging and models of democratic group leadership. Subadults were subordinate to adult females, and their relationships were characterized by high levels of aggression. This aggression was especially common during the first half of the coati year (Nov–April), and subadults were more peripheralized during this time period. Subadults likely chose spatial positions to avoid aggression and were actively excluded from the center of the group by adult females. In the Iguazú coati groups, it appeared that food acquisition and social agonism were the major determinants driving spatial choice, while predation played little or no role. This paper demonstrates that within-group spatial structure can be a complex process shaped by differences in body size and nutritional requirements, food patch size and depletion rate, and social dominance status. How and why these factors interact is important to understanding the costs and benefits of sociality and emergent properties of animal group formation.

Introduction

The within-group spatial position of animals is mostly influenced by feeding competition, predation threat, and social dominance (reviewed in Hirsch 2007a). In general, individuals in central spatial positions experience a lower threat of predation and an increase in feeding competition (Krause 1994; Krause and Ruxton 2002; Caro 2005). In moving groups, individuals at the front edge typically undergo higher predation threat and foraging success compared to the back of the group (Busse 1984; Janson 1990b; Bumann et al. 1997; Carbone et al. 2003; Di Blanco and Hirsch 2006; Romey and Galbraith 2008). This pattern arises due to increased predator encounter rates at the front of the group and food depletion from the front to back of the group. Alternately, contest competition can lead to increased feeding success in the center of the group, which

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has been found in several species (Robinson 1981; van Schaik and van Noordwijk 1986, 1988; Janson 1985, 1990b; Barton 1993; reviewed in Hirsch 2007a).

In some cases, within-group spatial choice is largely driven or constrained by social interactions and dominance status. Several studies have reported a correlation between dominance status and centrality (Robinson 1981; Janson 1985, 1990a; van Schaik and van Noordwijk 1986; Rayor and Uetz 1990; Clifton 1991; Flynn and Giraldeau 2001; Krause 1994; Ron et al. 1996). Janson (1985, 1990a, b) emphasized that feeding ecology could drive these patterns. In many studies of frugivorous primates, centrality in the group often equates to being inside a fruit tree, during which time subordinates are often excluded from the food patch (Vogel and Janson 2007).

Hemelrijk (1998, 2000) noted that patterns of group geometry could arise from simple social processes, such as subordinates moving away from dominants after aggressive encounters. Using individual-based computer models, Hemelrijk (1998, 2000) found that dominants were predicted to be more central while subordinates should be peripheralized as a result of aggressive interactions. If spatial centrality of dominants can arise in the absence of predation and feeding competition effects, these computer models are an important insight into the origin and formation of within-group spatial preferences. However, it must be noted that the dominance relations that Hemelrijk modeled are typically driven by feeding competition; thus, the two factors are often inexorably linked. Although the avoidance of dominants may be an important proximate factor in determining spatial position, the underlying cause in most cases is presumed to be feeding competition. In an interesting counterexample, Ron et al. (1996) found that competition for central spatial positions in baboons was not related to food, but for spatial positions that were safer from predation.

The purpose of this study was to determine the relative importance of dominance, feeding competition, and predation on the spatial structure of ring-tailed coatis (*Nasua nasua*). Iguazú is an interesting study area because feeding ecology played an unexpected role in relation to foraging success and within-group spatial position. When coatis fed on small ground-litter invertebrates, no front-to-back food depletion was found (Hirsch 2010). During fruit feeding, feeding success declined from the front to the back of the group. This may be related to the rapid depletion times of many of the fruit trees fed upon by coatis, which would have led to a reduction in the amount of fruits available to late-arriving coatis (Hirsch 2009). Coatis spent most of their foraging time searching for ground-litter invertebrates but typically visited several fruit trees per day (Hirsch 2009, 2010). Paradoxically, the ability to arrive at fruit trees first was driven by spatial choice during invertebrate foraging. Because fruit trees were regularly visited and quickly depleted, coatis at the front of the group during invertebrate foraging were typically the first to arrive at fruit trees (Hirsch 2010).

A previous study of white-nosed coati (*Nasua narica*) spatial position preferences reported that adults typically ranged on the periphery of the group during terrestrial invertebrate foraging while the smaller, more vulnerable juveniles were located in the center (Russell 1979). Russell concluded that this pattern was a response to predation because the most vulnerable individuals ranged in the center of the group. The effects of feeding competition and predation on within-group spatial position do not solely differ between the center and periphery but also depend on whether an individual is located in the front or back of the group (Di Blanco and Hirsch 2006; Hirsch 2007a). Previous work on the Iguazú study population found that individuals at the front edge of the group spent significantly more time vigilant compared to all other spatial positions, indicating a particularly high threat of predation at the front edge of the group (Di Blanco and Hirsch 2006).

The unusual system of dominance in ring-tailed coatis may also play a large role in determining spatial position preferences and constraining the choices available for certain age/sex classes. Juvenile ring-tailed coatis were found to win agonistic interactions against older, larger individuals (Hirsch 2007b). This behavior was reinforced by coalitionary support from adult females who often directed aggression towards any older coati who fought with a juvenile (Hirsch 2007b). This aggression was particularly severe between adult females (coatis 2 years or older) and subadults (coatis between 1 and 2 years of age) during November–April, when the newborn juveniles were younger and more vulnerable. This seasonal increase in aggression allows juveniles to have priority access to food resources and free choice of within-group spatial positions (Hirsch 2010). Conversely, if subadults attempt to avoid violent confrontations with adult females, their spatial choice may be constrained to areas where adult females are not present.

These considerations lead to the following hypotheses:

Hypothesis 1. If predation was the principal factor driving spatial patterns, small juveniles which are more vulnerable to predation should be more central than other age/sex classes and should rarely be found at the front edge of the group.

Hypothesis 2. Individuals on the front edge of the group during invertebrate foraging arrived at fruit trees first and had higher feeding success on fallen fruit. If feeding success was the primary force driving spatial position preferences, it is predicted that the highest-

ranking age/sex classes (juveniles and adult males) would be found on the front edge of the group more often than other age/sex classes.

Hypothesis 3. If spatial patterns were driven exclusively by agonistic interactions, low-ranking subadults are predicted to avoid areas of the group where they would encounter aggressive conspecifics. Because there were more agonistic interactions between subadults and adult females from November to April, it is predicted that subadults should avoid adult females more during the high-aggression season.

Methods

This study was conducted at Iguazú National Park, Argentina, between August 2002 and October 2004 (for details of the field site, see Brown and Zunino 1990; Di Bitetti 2001a, b). The park contains a full set of natural terrestrial coati predators (*Panthera onca*, *Puma concolor*, *Leopardus pardalis*, and *Eira barbara*), but aerial predators are rare or absent (*Harpia harpyja*, *Spizaetus ornatus*, and *Spizaetus tyrannus*) (Di Bitetti et al. 2006; Di Blanco and Hirsch 2006). The two coati groups included in this study ranged from nine to 29 individuals (Table 1). To locate the groups, one to three adult females per group were fitted with radio-collars. Coatis were captured using Tomahawk or similar traps, anesthetized, and either fitted with radio-collars or given a unique combination of multi-colored plastic ear tags for individual identification (Dalton Rototags). Ear tags were placed on juveniles older than 4 months of age, and it was possible to individually recognize all group members older than 4 months of age. Groups of coatis were usually habituated within 2 to 3 weeks. Habituated coatis would allow observers to silently walk within 2 m of a focal animal without disturbing their behavior.

Individual focal samples were taken on known individuals from two groups (PQ and PSG) from August 2002 until October 2004. The group composition changed over time, and subadults were only present in the PQ group during 2003, and the PSG group during 2004 (Table 1). Ten second individual focal samples were recorded, and the same individual was not resampled within 10 min. During the focal sample, I recorded the identity of the focal individual, within-group spatial position, individual and group activity, individual and group terrestriality, group speed, the number and identity (when possible) of all individuals within 3 m of the focal, and the number of food items ingested. Short focal samples were used because many of the associated variables recorded during the focal samples changed frequently (particularly the density of neighbors within 3 m). Individuals were selected opportunistically. Due to poor overall visibility in the dense forest, it was not feasible to select individuals based on a pre-determined order. Adults were preferentially targeted over juveniles, especially during 2004 when both groups had large numbers of juveniles.

Spatial position of individuals was recorded in the same manner as Janson (1990a, b). The group spread was visually divided into three concentric circles or ellipses: (1) center, (2) middle, and (3) edge, each representing one third of the total diameter. The location of coatis within these circles was then further subdivided into 12 positions based on the number of a clock, with 12 being the front-most position and six representing the back of the group. These 36 spatial positions were then collapsed into five spatial position categories (see figure in Hirsch 2010): (1) front edge, (2) front middle, (3) center, (4) back middle, (5) back edge. The average length and width of the two groups were 23.23 by 14.34 m, respectively (Hirsch 2010).

Statistical analyses

The number of samples recorded for each age/sex class varied due to differences in the number of individuals in each age/sex class and opportunistic sampling. Unequal sample sizes were recorded for each spatial position because the area of outer spatial positions was larger than inner spatial positions and because coati density varied by spatial position (sample size for spatial position: (1) front edge=1,423, (2) front middle=731, (3) center=740, (4) back middle=652, (5) back edge=928). When coati groups were at a fruit tree, the group spread was often smaller, and the density of individuals increased. To control for any possible effects of fruit feeding on spatial position preferences, only samples taken during invertebrate

Table 1 Group membership for the PQ and PSG during the study period

Subadults are individuals between 12 and 24 months of age. Juveniles are between 2 and 12 months old

Group	Year	Adult males	Adult females	Subadults	Juveniles	Total group size
PQ	2003	1	3	2	9	15
	2004	0–1	5	0	22–24	27–29
PSG	2003	0–1	3–5	0	6	9–12
	2004	1	5	6	15–17	27–29

foraging were used in this analysis (see Hirsch 2010 for fruit foraging results). Because spatial position during invertebrate foraging is the better predictor of whether an individual will arrive at a fruit tree first, using spatial position data while feeding on invertebrates should be the best test for comparing the effects of feeding competition, predation, and aggression. Samples from the two groups were combined into one dataset after an initial analysis indicated that spatial preferences did not differ between groups. In order to test whether age/sex class had a significant effect on spatial position, the focal samples were entered into a contingency table with four age/sex classes and five spatial positions ($N=20$ cells). To test for changes over time and different levels of agonism between adult females and subadults, the dataset was divided into two seasons, resulting in two contingency tables. Levels of aggression between adult females and subadults of both sexes changed over time. Higher amounts of aggression were observed during the first half of the coati year, which corresponds to when the juveniles first entered the groups until they were 6 months of age (November–April). During the latter half of the coati year (May–October), aggression was less severe (Hirsch 2007b). Expected cell-wise values were calculated for each age/sex class and spatial position based on the total number of samples recorded for each age/sex class and the total number of samples recorded at each spatial position. The relative deviations from these expected values were calculated by subtracting the observed values from the expected values and then dividing these by the expected values. G tests were used to test whether the observed spatial position distribution of different age/sex classes was different from random. If the G test P value for an age/sex class was <0.05, cell-wise χ^2 values were calculated for each age/sex class and spatial position combination. With the exception of adult males, all χ^2 tests for homogeneity were significantly different than expected. The cell-wise relative deviations were then graphed for each age/sex class.

A separate analysis was conducted to measure spatial association patterns within and between certain age/sex classes. Association indexes were created using data from the two group years when subadults were present (PQ 2003, PSG 2004). Association matrixes were constructed using individual focal samples in which all individuals within 3 m were identified ($N=3,731$). Two matrices per year were constructed to test for the effects of changes in aggression level over time (high- versus low-aggression season). Because of a delay in marking the PSG juveniles during 2004, the first PSG matrix during 2004 does not include juveniles. The total number of neighbors observed within 3 m for each age/sex class during the focal samples was summed and divided by the total number of group

members which could have been a neighbor to the focal (group size minus one). This number was then multiplied by the number of members of each age/sex class to determine the predicted number of individuals in each age/sex class which should have been observed within 3 m of the focal. The symbol α equals the particular age/sex class analyzed.

Expected # neighbors of α age/sex class

$$= \left(\frac{\text{\# of all neighbors observed} < 3\text{m}}{\text{\# of individuals in group} -1} \right)$$
$$\times \text{ \# of individuals of } \alpha \text{ age/sex class}$$

This association index was then summarized for each age/sex class to determine whether some age/sex classes were found in close proximity to other age/sex classes more or less often than predicted. Samples recorded for each age/sex class were analyzed using G tests to determine whether the distribution of observed neighbor associations deviated from the expected values. Proportional deviations from expected values were calculated by subtracting the expected number of neighbors by the observed number of neighbors for each age/sex class and then dividing this value by the expected number of neighbors. Cell-wise P values were then calculated for each age/sex class, but only if the P value for the overall test for heterogeneity was <0.05.

Results

With the exception of adult males, the spatial distribution of each age/sex class was significantly different from random (G test χ^2 value >9.488, $df=4$). Juveniles were found more frequently in the front edge spatial position and less likely in the back edge position (front edge deviation=0.111, $\chi^2=4.662$, $P=0.031$, back edge deviation=−0.314, $\chi^2=20.616$, $P<0.001$). Juveniles were not expected to shift spatial position preferences over time based on the amount of aggression between subadults and adult females; thus, data from all 12 months were used for juveniles. The spatial patterns of adult females and subadults changed over time (high-aggression season: total model $R^2=0.021$, $N=1,472$, $df=12$, $\chi^2=95.187$, $P=<0.001$; low-aggression season: total model $R^2=0.007$, $N=1,957$, $df=12$, $\chi^2=44.546$, $P=<0.001$). During the high-aggression season, adult females and subadults exhibited more pronounced spatial position preferences than during the latter part of the year (Figs. 1 and 2). Adult females were more central in the group and less peripheral during the high-aggression season. The spatial distribution of subadults during the high-aggression period was the opposite of the adult
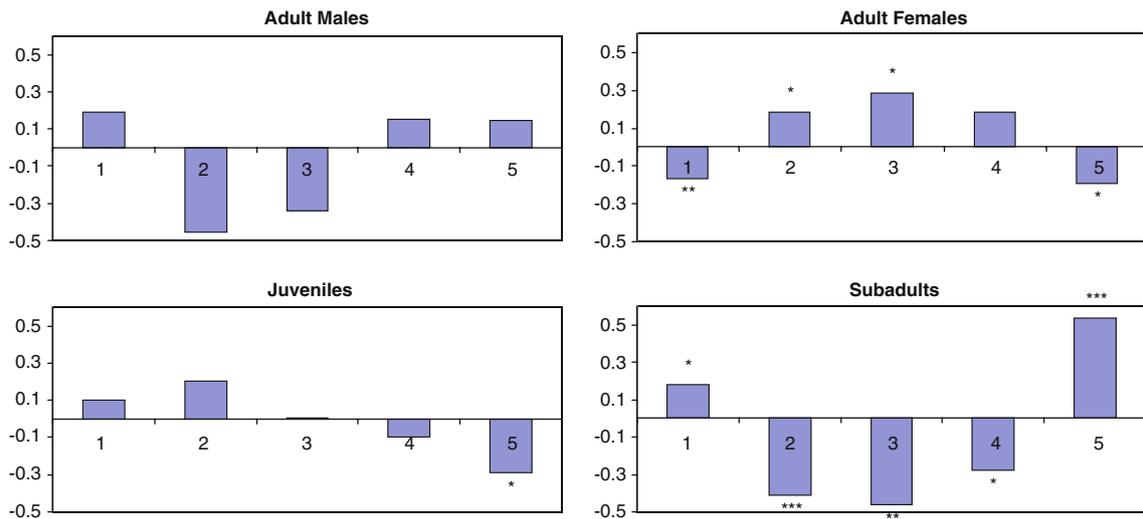
Fig. 1 Deviations from expected values of within-group spatial position during the high-aggression season, November–April. Spatial positions *1*=front edge, *2*=front middle, *3*=center, *4*=back middle, *5*= back edge. *$P \leq 0.05$, **$P \leq 0.01$, ***$P \leq 0.01$. Total model R^2=0.021, *df*=12, χ^2=95.187, *P*=<0.001, *N*=1,472

females; they were less likely to be in central spatial positions and more likely to be peripheral (Fig. 1). During the season of lower aggression, both adult females and subadults were often located at the back edge of the group (Figs. 1 and 2).

The density of individuals within 3 m of the focal individual varied depending on the location inside the group. The average number of neighbors was highest in the center compared to peripheral spatial positions, and individuals in the front had more neighbors than individuals in the back of the group (average number of neighbors within 3 m; front edge=1.50, front middle=2.34, center= 3.03, back middle=1.63, back edge=1.18). The number of

neighbors within 3 m differed by age/sex class (Kruskal–Wallis test, χ^2=56.00, *df*=3, *P*<0.001) and by season (χ^2= 59.00, *df*=1, *P*<0.001) (Fig. 3). The most notable difference was that adult females had many more close neighbors when their offspring were young compared to when offspring were 6 months of age or older (χ^2=96.00, *df*=1, *P*<0.001).

The age/sex class composition of near neighbors of adult females, subadults, and juveniles were all different from the predictions based on group composition (Table 2). Adult females and subadults were always found in close proximity less than predicted, with the exception of PQ group subadult neighbors during the latter half of 2003. The skew in neighbor preferences for adult females and subadults was
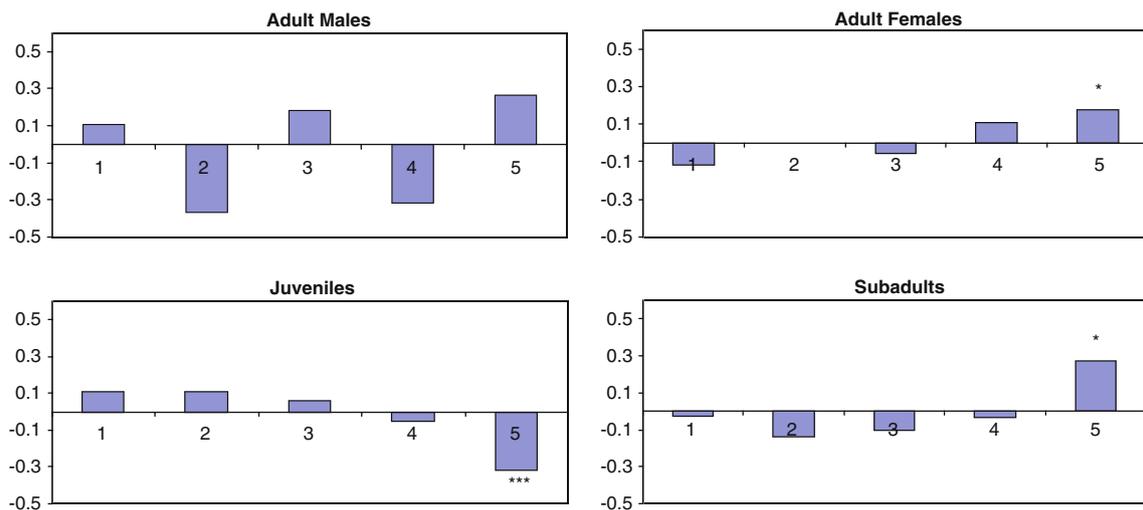

Fig. 2 Deviations from expected values of within-group spatial position during the low-aggression season, May–October. Spatial positions *1*=front edge, *2*=front middle, *3*=center, *4*=back middle, *5*=back edge. *$P \leq 0.05$, **$P \leq 0.01$, ***$P \leq 0.001$. Total model R^2= 0.007, *df*=12, χ^2=44.546, *P*=<0.001, *N*=1,957
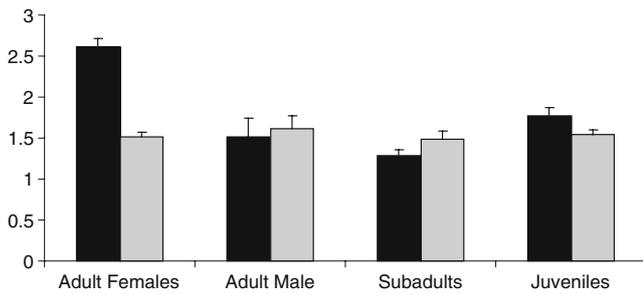
Fig. 3 Average number of neighbors within 3 m of each age/sex class (±SE). The *black bars* correspond to the high-aggression season (November–April), and the low-aggression season (May–October), *striped bars*

greater during the period in which juveniles were 6 months of age or younger compared to the latter half of the year. In general, each age/sex class was found with other members of the same age/sex class more often than predicted (Table 2). A seeming exception to the pattern of age/sex class cohesiveness was the pattern found during the latter half of 2004 in the PSG group. During this time, both subadults and adult females were found to be negatively associated within their own age/sex classes. In this case, an exceptionally large

number of juveniles, which often clustered together, may have skewed the results of other age/sex classes.

Discussion

Hypothesis 1: predation and spatial position

There is little evidence that predation was the major factor shaping within-group spatial position preferences in ring-tailed coatis. If predation was a major factor, juveniles should have been found on the front edge of the group less often than other age/sex classes and more frequently in the center of the group. This hypothesis was not supported, and juveniles were found on the front edge of the group more often than predicted. A previous study of white-nosed coati spatial position in Panama found that juveniles were more often located in the center of the group, and it was concluded that adult peripherality functioned to protect juveniles from predators (Russell 1979). This mechanism was clearly not driving adult female spatial preferences in Iguazú because adult females were found in the center of the group more often than predicted, especially when juveniles were younger and more vulnerable.

Table 2 Deviations from expected summed pair wise associations for each age/sex class

	Adult male		Adult females		Subadults		Juvenile		Number of focal samples
	Deviation	P	Deviation	P	Deviation	P	Deviation	P	
Group PQ, high-aggression season, March–April 2003									
Adult male	–	–	−0.129	–	0.307	–	−0.025	–	75
Adult females	−0.677	<0.001	0.085	<0.001	−0.624	<0.001	0.103	<0.001	735
Subadults	0.195	0.026	−0.175	<0.001	1.732	<0.001	−0.156	<0.001	164
Juveniles	−0.383	<0.001	0.532	<0.001	−0.244	<0.001	0.750	<0.001	672
Group PQ, low-aggression season, May–October 2003									
Adult male	–	–	0.00	–	−0.250	–	0.056	–	28
Adult females	−0.553	0.002	0.005	0.593	−0.181	0.003	0.100	<0.001	188
Subadults	−0.451	0.029	0.190	0.003	0.647	<0.001	−0.085	0.001	102
Juveniles	−0.563	<0.001	−0.114	<0.001	−0.192	<0.001	0.161	<0.001	416
Group PSG, high-aggression season, December 2003–April 2004									
Adult male	–	–	0.074	–	−0.062	–			43
Adult females	0.704	<0.001	0.214	<0.001	−0.260	<0.001			213
Subadults	−0.465	<0.001	−0.513	<0.001	0.606	<0.001			226
Group PSG, low-aggression season, May–October 2004									
Adult male	–	–	−0.017	–	−0.058	–	0.021	–	83
Adult females	−0.306	0.007	−0.289	<0.001	−0.151	<0.001	0.139	<0.001	346
Subadults	−0.568	0.010	−0.222	<0.001	−0.317	<0.001	0.173	<0.001	222
Juveniles	−0.339	<0.023	−0.295	<0.001	−0.394	<0.001	0.244	<0.001	218

Rows represent the focal individuals and columns represent the deviations from predicted pair wise associations. Each age/sex class was tested for heterogeneity for each time period (e.g., each row) using G tests. With the exception of adult males, the distribution of neighbors for all age/sex classes differed from expected for all years ($df=3$, G test $\chi^2 >7.815$). In every year, adult males did not significantly differ from expected ($df=2$, G test $\chi^2 <5.991$). The cell-wise P values for adult males were not reported to reflect this lack of overall significance

The population density of medium- and large-sized ground predators (ocelots, puma, jaguars) in Iguazú is generally lower than most comparable tropical forest sites (Di Bitetti et al. 2006; Kelly et al. 2008; Paviolo et al. 2008; Hirsch 2009). If the number of predators and threat of predation is low, juveniles in Iguazú may have no need to locate themselves in the group center. A previous study of coati vigilance in Iguazú contradicts this hypothesis. Because levels of anti-predatory vigilance were much higher at the front of the group than all other spatial positions, coatis likely perceive that the front edge of the group is the most dangerous spatial position (Di Blanco and Hirsch 2006). Even though the front edge of the group is perceived to be the most dangerous spatial position, juvenile coatis were frequently found in the front edge of the group; thus, foraging benefits may have outweighed the increased risk of predation in this population. Ideally, further studies of coati vigilance behavior and spatial position preference could be conducted in field sites with higher predator densities to shed more light on this issue.

Hypothesis 2: feeding competition

Higher feeding rates at the front edge spatial position have been found in a large variety of species, including this population of coatis (Krause and Ruxton 2002; Hirsch 2010). If feeding competition was the main factor determining within-group spatial position, dominant juvenile coatis should have been found at the front edge of the group more than lower-ranking age/sex classes. Juveniles likely chose front edge spatial positions during invertebrate foraging to arrive at fruit resources before other age/sex classes. By arriving first, the juveniles were able to consume more and possibly higher-quality fruit than those who arrived later. It was common to observe a large number and density of juveniles at the front edge of the coati groups during foraging and travel, while the other age/sex classes mostly trailed behind. This resulted in a higher density of individuals at the front edge of the group compared to the back edge.

If a positive correlation existed between dominance rank and the choice of front edge spatial positions, subadults should have been found at the front edge less than all other age/sex classes. During the high-aggression season, the opposite pattern was found, and subadults were located at the front edge of the group more often than predicted. Subadults appeared to use a bimodal spatial position strategy (cf. non-tolerated adult capuchin monkeys: Janson 1990a). They either ranged at the front of the group or the back, but rarely the center. When at the front, subadults were sometimes able to arrive at fruit trees before others but were often forced to leave when adult females arrived (Hirsch 2007c, 2010). Subadults were most often found at

the back edge of the group throughout the year. In this back edge location, subadults could eat whatever food the rest of the group did not consume, while simultaneously avoiding aggression. The patterns found in this study indicate that the spatial choice of subadults was mostly shaped by social constraints (e.g., exclusion from the center of the group). Alternately, subadults could have been shifting their spatial preferences to match more complex mechanisms of feeding competition (Hirsch 2007a, 2010).

Adult males were not found at the front edge of the group more often than other age/sex classes, and adult males were found at fruit trees less frequently than all other age/sex classes (Hirsch 2010). These results are surprising because adult males are generally dominant to all other age sex classes (Hirsch 2007b). This latter conclusion may be misleading because dominance rank was based on dyadic contests, and adult males may be subordinate to other age/ sex classes during coalitionary interactions. In some cases, multiple adult females were seen chasing an adult male (Hirsch 2007b). In white-nosed coatis, adult females and their offspring have been observed forming coalitions against adult males and chasing them from fruit tree shadows (Gompper et al. 1997). The avoidance of fruit trees may be connected to an increased risk of being a victim of coalitionary aggression during feeding at these clumped, high-valued food resources (Hirsch 2010).

Hypothesis 3: social effects on spatial position

Many of the observed patterns of spatial position preference appear to have been heavily influenced by social factors. In particular, subadults were less likely to be found in the center of the group during the high-aggression season, which is where the adult females were most often found (Fig. 1). The center was not the area with the most food; thus, the area where subadults faced the largest risk of aggression was different from the best location for higher feeding success. Subadult avoidance of adult females was also reflected in the proximity data, wherein adult females and subadults occurred as neighbors less often than predicted during the high-aggression season (Table 2). These patterns corresponded to observations that, when juveniles first entered the group, subadults were chased from or actively avoided areas where adult females were found (Hirsch 2007b). This behavior probably served to reinforce the newly subordinate status of subadults who were dominant a few months prior. This seasonal increase in aggression influenced patterns of spatial preference and limited the spatial preference options available to subordinate subadults. Once levels of aggression subsided, the subadults no longer strictly avoided being close to adult females, and the subadults were less constrained in their choice of spatial position.

Conclusion

The observed patterns of coati spatial position preference partially mirror conclusions from Janson (1990a, b) who found that dominant capuchin monkeys (the alpha male and female) chose spatial positions that maximized their feeding success and the least tolerated individuals stayed in peripheral spatial positions despite higher predation risk and at best mediocre foraging success. However, in Janson's study, the most vulnerable individuals preferentially stayed close to the center of the group unlike ring-tailed coatis. In ring-tailed coatis, food acquisition and social competition appeared to be the major factors driving spatial position preference and not predation. These patterns could have been influenced by relatively low predator densities. The observation that juvenile spatial choice was most influenced by food acquisition may be due to a high reproductive rate (four to six offsprings per year) and the need for juveniles to grow very rapidly in a short time period. If this greater drive to acquire resources was the major factor causing juveniles to locate themselves in risky spatial positions, it is predicted that these patterns may be found in other mammal species with relatively fast life histories. The presence of juveniles on the front edge of the group may have important consequences with respect to group leadership. If group leadership is democratic and overly influenced by individuals on the front edge of the group, as assumed in many models, the youngest and presumably most naïve individuals in the group were responsible for group leadership (Couzin et al. 2005; Conradt and Roper 2007; Dyer et al. 2008). This would be one of the first recorded examples of "leading by need" (Conradt et al. 2009). Alternately, mature adult females could have been able to influence group decisions from the center of the group using vocalizations or some other mechanism (Boinski 2000). Given the frequent contact vocalizations given by coatis, the latter hypothesis is highly plausible and should be studied in more detail.

Ethical standards This study complied with all laws and regulations of Argentina, the Administración de Parques Nacionales, and ASAB/ABS guidelines for animal welfare.

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